SPIDER COMMUNICATION

Mechanisms and Ecological Significance

Edited by Peter N. Witt and Jerome S. Rovner

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In the last ten years a large number of published papers have reported for the first time results of the application of modern scientific technology to the investigation of spider physiology and behavior. Concentrating on the complex spider communication system, this book assembles the most recent multidisciplinary advances of leading researchers from many countries to assess the peculiar role spiders play in the animal kingdom. Here the various contributors review their discoveries, place them within the general field, and speculate on the advantages and disadvantages that special development has provided for spiders.

Topics covered and their authors are: significance and complexity of spider communication (Bertrand Krafft); vibratory signals (Friedrich G. Barth); acoustic communication and reproductive isolation (George W. Uetz and Gail E. Stratton); visual communication in jumping spiders (Lyn Forster); communication behavior in jumping spiders (Robert R. Jackson); chemical communication in Lycosids and other species (William J. Tietjen and Jerome S. Rovner); social spacing strategies (J. Wesley Burgess and George W. Uetz); and foraging (Susan E. Riechert and Jadwiga Łuczak).

Peter N. Witt was formerly Chief of Mental Health Research, Department of Human Resources, State of North Carolina.

Jerome S. Rovner is Professor of Zoology at Ohio University.

Chapter 1

INTRODUCTION: COMMUNICATION IN SPIDERS

Peter N. Witt

North Carolina Mental Health Research
Anderson Hall
Dorothea Dix Hospital
Raleigh, North Carolina 27611

Most of the authors of this book were invited by me to come together as part of the International Meeting sponsored by the American Arachnological Society in the summer of 1978 in Gainesville, Florida. They agreed to discuss their work as it contributed to our knowledge about communication in spiders. I conceived the plan for the book at the symposium and thus became its senior editor. At a later date I asked Jerome Rovner to join me in the editorial work, and we bear together the responsibility for the present list of contributors and the present shape. The final version developed after the symposium through additional reviews of the relevant literature and inclusion of current laboratory and field work. All along we tried to preserve the attraction of the immediateness of the reports from the authors' own laboratories and combine them with a more general review of the field. The text aims at presenting the present state of knowledge and is a compromise between completeness and readability. Sometimes a chapter fits only the widest definition of "communication," e.g., Riechert and Łuczak's "Spider Foraging: Behavioral Responses to Prey." Because it contains valuable information on spider behavior and ecology which is not to be found summarized elsewhere, and because it rounds off the other chapters by applying some of the sensory physiology and other knowledge to predator-prey interactions, the editors decided to include it. After all, the subject matter of that chapter is an important part of the spider's relationship with its environment. A special effort is made to address readers beyond arachnologists, so that they can sample and compare how much (or little) is known about one aspect of this one group of animals at the present time.

To many readers opening this volume, the title will seem strange, if not unworthy of serious and lengthy treatment. On the face of it, spiders do not deserve reputations for communicability. Rather, they are popularly regarded as solitary and silent predators, who neither seek, nor are likely to obtain, partners in any gentle exchange. A moment's reflection will revise that judgment, but it is probably the first task of an introduction to offer some explanation of why the volume is thicker than one might anticipate. The events of courtship would probably be granted at once to be a matter of communication. Even the "news" which prey provides, however regretfully it does so, could be construed as communication. Indeed, this latter, very broad interpretation of the term "communication" is the one I have chosen to use in order to include material in this volume which is relevant to a consideration of mechanisms underlying communication *sensu strictu*. Thus, even where the research dealt with a system for prey detection, the findings of such a study could also be of interest to those seeking to understand the use of the same channel for signaling by a male spider when courting a female.

For the reader who pictures only the solitary web-builder, there will be surprises in this book, especially when communal spiders are considered. But the topic is capable of even wider expansion; so much so that in preparing this book one became convinced that to cover the problem thoroughly, it will never be thick enough. Scarcity of knowledge, rather than lack of subject matter worthy of discussion, has limited the size of the present work. In the search for knowledge, this book is a way station where we review how far we have come in order to determine where we want to go.

Invertebrates have recently become particularly interesting to neuroscientists. Chase (1979) points out that papers in invertebrate neurobiology constituted the third largest of 41 topical categories at the 1978 meeting, which represented the whole Society of Neuroscience's interest. He discusses the advantages of relatively fewer neuronal elements for identification in invertebrates, together with greater technical accessibility. This accounts for the fact that physiological descriptions of behavioral control are more complete for invertebrate models than they are for vertebrate models. If one assumes evolutionary continuity from animals to man, it follows that studies of identification of the role of particular neurons in invertebrates become relevant to the human situation. This in turn permits more enlightened speculation on the mind-body problem (see Chase, 1979).

Spiders, one of several groups making up the class Arachnida, are invertebrates which show a number of peculiarities. An example of the special body structure of spiders is shown in Figure 1.1. Spiders show a number of precoded behavior patterns, frequently called fixed action patterns. In several places in this book such behavior

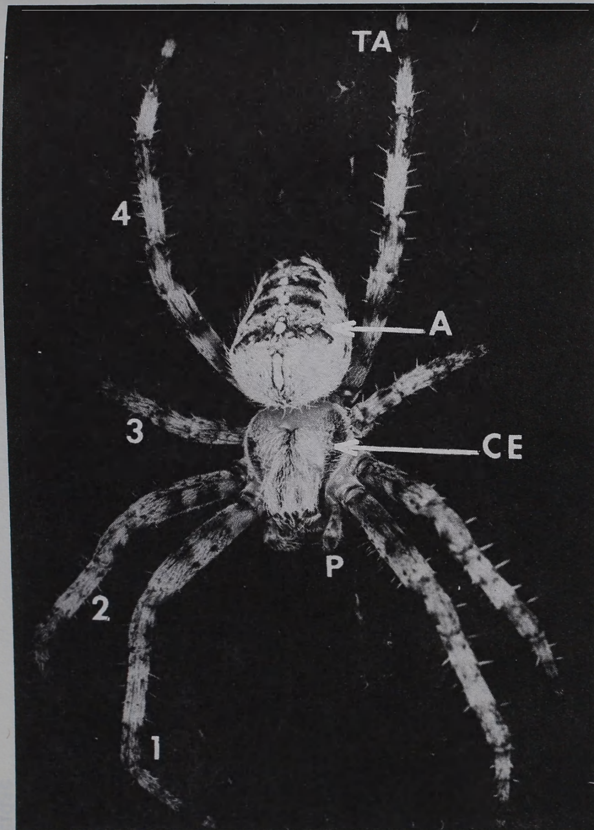

FIGURE 1.1a. Dorsal view of *Araneus diadematus*, the cross spider, hanging face-down in its orb-web. Numbers 1, 2, 3, and 4 designate the first, second, third, and fourth right legs, respectively. P: pedipalp; CE: cephalothorax; A: abdomen; TA: tarsus of fourth left leg. Note that, in contrast to insects, the spider has a two-part body, four pairs of legs, and a pair of pedipalps instead of antennae. FIGURE 1.1b. Scanning electron micrograph of the ventral view of the same spider (face-down as in 1.1a). C: chelicera with fang; P: pedipalp; S: sternum (on the ventral side of cephalothorax); A: abdomen; CO: coxa; T: trochanter; F: femur of fourth leg.

patterns as courtship, web-building, and feeding will be described as highly ritualized and species-specific. The neuronal substrates of such behavior probably will be elucidated one day. The following chapters review much of the present knowledge as an early step in this process. Table 1.1 lists the families of spiders containing one or more species whose names will appear in these chapters.

Why do we focus on communication? Communication is important for an animal's survival. Animals change their behavior as a consequence of the information they receive. In social animals all communal life is based on a communication network, which car-

TABLE 1.1. Families of spiders included in this book.

Web-weavers	*Wanderers*
Agelenidae - funnel weavers	Anyphaenidae
Amaurobiidae	Archaeidae
Araneidae - "ordinary" orb-weavers	Clubionidae - sac spiders
Argyronetidae - water spiders	Ctenidae
Atypidae - purse-web spiders	Dysderidae
Barychelidae	Gnaphosidae (Drassidae)
Ctenizidae - trapdoor spiders	Lycosidae - wolf spiders
Dictynidae	Mimetidae - pirate spiders
Diguetidae	Oxyopidae - lynx spiders
Dinopidae - ogre-faced spiders	Philodromidae
Dipluridae - funnel-web tarantulas (mygalomorphs)	Pisauridae - nursery-web spiders
Eresidae	Salticidae - jumping spiders
Filistatidae	Scytodidae - spitting spiders
Hahniidae	Sicariidae
Hypochilidae	Sparassidae (Heteropodidae) - huntsman spiders
Leptonetidae	Theraphosidae - "ordinary" tarantulas (mygalomorphs)
Linyphiidae - sheet-web weavers	Thomisidae - crab spiders
Liphistiidae	
Loxoscelidae	
Micryphantidae (Erigonidae) - dwarf spiders	
Ochyroceratidae	
Oecobiidae	
Pholcidae - long-legged spiders	
Segestriidae	
Tetragnathidae - long-jawed orb-weavers	
Theridiidae - comb-footed spiders	
Uloboridae	
Urocteidae	

ries information among the individuals, letting each know what it has to do to assist in the survival of relatives and thereby insure its own best genetic interest. Communication between sexually reproducing animals is one prerequisite for their genes' survival.

There are many ways in which living beings communicate. Some of the ways are so characteristic for a species or genus that they can be used for defining the difference between that group and others. Humans are frequently distinguished from animals by the ability of our species to use language for communication. The more recent investigations of chimpanzees' ability to master and apply American Sign Language are efforts to resolve the controversy over the degree of sophistication, abstraction, and generalization which these apes can develop in this communication medium as compared to humans (Griffin, 1977, 1978; Premack and Woodruff, 1978).

Understanding communication between living beings requires insight into many different aspects of life. The organs which transmit and receive signals can be studied as to their physical appearance and particular function. The signal itself—its variation, nature, means of transmittal, and its information content—is another subject for investigation. These components cannot be understood as part of the communication process if the meaning of the message is not clarified: how it was encoded by the communicator and how it was decoded and interpreted by the receiver. Usually, observation and the measurement of the individual's behavior under specified conditions are used as methods for gaining some understanding of the content and meaning of a communication process.

The central position which communication plays in animals' lives can be deduced from the observation that studying communication leads to an understanding of the peculiarities of that animal and its conspecifics. The description of a simple experiment will illustrate the point.

A spider hangs face down in the center of its intricate orb web. A low-frequency tuning fork is struck. As soon as the vibrating prongs of the instrument touch a radius of the web, the spider turns and positions one front leg on the moving radius (Figure 1.2). This trial can be repeated over and over, and the results will nearly always be the same. Further reaction is more variable and depends on a number of circumstances: the duration of the signal, the response of the web to short jerks on the radius by the first legs, the spider's appetite, the number and character of preceding trials, and even general circumstances such as time of day, sun, wind, and rain.

FIGURE 1.2. A vibrating tuning fork is brought into contact with one radius at the periphery of the orb-web of an adult female *Araneus diadematus*. The animal orients toward the vibrating radius and probes with its front legs to monitor the stimulus.

What has just been described represents certain aspects of communication (broadly defined) which are characteristic of many species of spiders. The tuning fork produced a measurable signal; frequency, intensity, and variability of the signal could have been tested for the ranges in which they elicit a response. The instrument was used in place of another animal—a conspecific or prey—to test the nature, frequency, and intensity of effective signal production. The signal was transmitted through a specific channel, in this case mechanically through the silken radial thread. The channel connected the signaler with the receiver. The resulting behavior of the spider, i.e., turning in the direction of the tuning fork, provided evidence that the signal was received and decoded. The lyriform and slit organs on the legs of the spider (here *Araneus diadematus*) have been shown in other spiders to be sensitive to vibration-induced strains in the exoskeleton, as will be discussed by Barth. These receptors sent impulses (action potentials) along nerve fibers through the legs to the central nervous system. Here the message was decoded and translated into outgoing nerve-borne signals, which resulted in patterned muscular contractions that produced movements of the legs and body. All sections of this communication system worked together to produce an observable action-reaction sequence. As will be fully discussed in later chapters, the investigator can analyze the various parts of the system, and define the role each plays in the total process.

Beyond the general conception of communication which we have derived from this observation, it has taught us much about the animal in its living space. This particular spider, like many of its relatives, has made use of a specific signal quality, namely the vibration of the substrate on which it rests. Each type of signal, be it chemical, acoustic, visual or, as in this case, vibratory, has properties which make it practical for a specific environment. Vibration, for example, is independent of light and can be as effective at night as during the day. It is relatively independent of air currents, which can, on the other hand, carry chemicals with them. Nocturnal spiders, which build an invisible trap to catch visually orienting flies, were preadapted with a sensory system which is highly receptive, independent of vision. Many spiders have compensated for the absence of a suitable substrate over which a vibratory signal can be conducted, as well as for limitations in the distance of conduction in available substrates, by extending the perceptual range of the legs with a silken structure. It is not enough that the area of capture is enlarged; the fact of contact by the prey with the silk must be communicated. Suddenly the radiating shape of the web (Figure

1.2) takes on a new meaning for the observer: the web extends the perceptual range of the sense of vibration from about 15mm to more than 500 mm by forming a suitable substrate for the transmission of vibrations to the legs. The legs, in turn, improve reception by pulling the silk tight.

Knowledge of the organs for communication lets us understand other behaviors of the animal. During orb-web construction, the spider pulls and probes existing threads to gather information on the degree of completion, before new strands are laid (Peters, 1938; Reed, 1969). It straddles angles, apparently assessing their width and comparing them to an internal "plan" or template, which guides web construction. In the laboratory we have let the cross-spider build an orb-web in a closed box in complete darkness. Elaborate measurements carried out on the resulting webs showed no differences between these webs and those built by the same animal in partial light. No longer dependent on vision, and in darkness safe from visually searching predators, the spider builds an almost invisible web on which it will catch visually orienting prey.

Pertinent to the topic of communication is the fact that the web also plays a delicate and essential role in the spider's courtship behavior. A male may drum or pluck on the web of a female over long periods of time, until the aggressive attack of the female changes to acceptance of the male for copulation. It can be shown, by comparison of the webs of a few spider species (Risch, 1977), that the web built by the adult female is more species-specific than is the juvenile web. This observation holds for measures of size, fine structure, and shape. It raises the question of whether the specific resonance of the female web plays a role in species recognition for the "short-sighted" male. Blanke's (1973) experiments revealed reactions of males to wind which had blown across sexually mature females, suggesting that in finding the female web the male may be aided by an airborne signal, probably a chemical. This may then be followed by vibratory communication. Rarely is only one sensory modality involved in communication behavior; instead, one channel is usually predominant and others assist in one stage of communication. The roles may be reversed in the next stage.

It is not necessary to suppose that the spider has any conception of the world which she so nicely manages. In this respect, the condition bears some resemblance to the human condition. The world outside us, and the mental picture we have of it, is a product of what we can detect through our receptor organs and the subsequent analyses in the brain. We see colors and shades from which we guess at shapes and materials. We smell, feel, hear; and we use those inputs to recognize, categorize, understand objects and other living beings. Philosophers like Schopenhauer have gone so far as to describe the world as a product of our will and imagination.

Arthur Schopenhauer's principal work is the book *Die Welt als Wille und Vorstellung*, which appeared first in Leipzig in 1819, and was translated into English in 1883 under the title *The World as Will and Idea* (see ref. Schopenhauer). The second part of the title, which describes the first part of his philosophy, is of special interest here. The German word *Vorstellung* can also be translated as "representation, conception, mental image" (The New Cassell's Dictionary, 1958). Any of those three words appear to this writer to describe part of Schopenhauer's philosophy better than the common translation "idea." Based on Descartes, Kant, and Locke, Schopenhauer stressed the distinction between the phenomenon, or the appearance that a thing presents to the perceiving mind, and the thing as it is in itself. Through perception the mind is presumed to be aware only of the observable facts or events, i.e., of the phenomena: what lies behind them, being beyond all possible experience, is unknowable. It is impossible to dissociate conceptual thinking from the perceptual experience on which it is based. To use Schopenhauer's words (in translation): "Conceptions and abstractions which do not ultimately refer to *perception* [translator's italics] are like paths in the wood that end without leading out of it." In brief, our conception or understanding of the world is formed by the organs we have to perceive it; thus, we have a predominantly visual world. A very different world, mainly filled with touch and vibration signals, exists for the web-building spider. By discussing the spider's organs for communication, some of the contributors to this book try to introduce the reader to the "inner world" of the spider.

Such an argument is not intended to mean that the present author believes exclusively in the familiar "idea that there can be nothing in our intellect which has not entered it through our senses." We must assume that "every animal is born with expectations and anticipations" (Popper, 1974), which means that it possesses inborn knowledge. However, it is argued that observation of the perceptual repertoire of an animal (including the central nervous processing of signals) introduces some special understanding of the animal and its works, in our case of spiders, which cannot be gained otherwise.

So far the word "communication" has been used loosely; no definition has been given. We have talked about communication between living beings, thereby excluding communication processes inside one being, i.e., nervous or chemical signals which carry messages from one part of the body to another. We have excluded passive communication between an individual and its environment, i.e., the perception of and reaction to temperature changes can sometimes be called passive communication (E. O. Wilson, 1975). Internal messages and the impact of the environment will only be discussed so far as they affect communication processes between animals. There are many definitions of communication available (see Smith, 1977; Sebeok, 1977; Wilson, 1975). Each definition serves a specific purpose; they are not mutually exclusive, but rather complementary. For that reason, none has been singled out. Rather it has been left to the authors of the different chapters to choose the definition which best suits their approach to the overall theme of communication in spiders.

Special signals carry messages for communication (for exceptions see Smith, 1977, p. 13). Such signals have to be produced by an organ which is specially adapted for signal production. A number of conditions have to be fulfulled before a signal is actually sent out: the physiological stage of the signaling organism has to be right before the environment (or the partner) can elicit the signal. Both the state of the organism and the environmental releaser determine whether a signal is sent.

Some of the following chapters focus attention on the nature of the signal, i.e., they discuss airborne, chemical, and other modes of communication. In pulsed signals, for example, one may distinguish between frequency and intensity, find graded and stereotyped repertoires, and note the manner in which the beginning and end of the signal are determined by the signaler or the environment. However, very few messages depend on one channel of communication only. In humans the visual perception of the signaler's face joins with the tactile message of a handshake and the auditory message of a greeting to communicate "welcome." The quality of any one of these elements, or its absence, may radically alter the message. The problems raised by the spectrum of signals and their possible combinations require additional kinds of study, and are the concern of other chapters.

The message can only get across to another living being if that individual has an organ sensitive to the nature of the signal, a way to decode the message, and is ready to receive it. The study of receptor organs—their sensitivity and ability to discriminate—is combined with observation of the behavior of the receiver to reveal whether a message was received and what its significance was. Analysis of communication behavior requires a special line of investigation, at a level of analysis which is just as important for our understanding of communication as are the anatomy and physiology of the communicating organisms and the physics of signal production, transmission, and reception.

Another way to look at communication is to place it in the wider context of its contribution to the survival of the organism, i.e., to gauge its adaptive value (Burghardt, 1977). It is generally assumed that organisms which live communally, frequently in structured societies, use more and a greater variety of signals than do solitary animals. However, an animal which lives alone is still dependent on communication with conspecifics (and sometimes with animals of other species). One has to assume that the lonely spider of our example, in the middle of its orb-web, is at least occasionally interacting with other orb-web builders with whom she competes for prey.

Communication systems change throughout the lifetime of an animal as requirements to communicate differ. The tiny immature spiderling, its nutritional needs supplied by the yolk, probably has communication requirements different from those of the adult female, one hundred times heavier, sexually mature, and a voracious feeder (Burch, 1979). Such ontogenetic development in the communication system of spiders has been little studied, an exception being Aspey's (1975) study of ontogeny of display in a wolf spider. On the other hand, a type of communication like the visual signaling given and received by jumping spiders may vary from species to closely related species. Comparison of communication systems can assist in tracing the phylogeny of whole taxonomic groups of spiders.

Communication involves at least two, and frequently more than two animals. If there is no receiver for a message sent out by a display of an animal, communication cannot take place. There is always a mutual evolutionary advantage (Smith, 1977) involved in successful communication. Frequently it achieves a central social function. One can assume that the degree of social organization of a species can be measured by its use of intraspecific communication.

Finally, one may ask whether spiders have developed ways specific to them in which they communicate? Do their communication systems set them apart from other animals? In many, the production and daily use of silk has opened up for them a means of communication which only few other animals can rival. When some of that knowledge was reviewed several years ago, Witt (1975), focusing on the orb-web, found that a small amount of evidence went together with a large array of speculation and surmise.

Much has been discovered since that time, and some chapters in this book update our knowledge of various aspects of spider communication.

The reader may be convinced by now that there is a good case for bringing together much of the existing knowledge about this topic. By reviewing communication in spiders—the organs involved, the purposes which communication serves, the circumstances under which it takes place, and the effect it has—we will increase our understanding of the more than 30,000 species of spiders (Levi and Levi, 1968) as much as we would by a review of their size, shape, and color. One may even be convinced that several authors are necessary to bring all the pieces of knowledge together in order to make it possible to understand fully the peculiarities of spiders and the relationship of species with each other. Platnick (1971) stresses that stereotyped patterns (e.g., courtship behavior) must be considered at least as important a character for systematics as morphology. But one can still ask whether the beautifully illustrated large books, like the recent volume by Gertsch (1979) on *American Spiders*, do not sufficiently cover the subject. The material presented in our book is so different from that discussed in other "spider books" (see references) that it can serve as a complement to these without repeating any of their details. Indeed, only the ten-page review by Weygoldt (1977) on "Communication in Crustaceans and Arachnids" has tried anything similar to this book and did so, of necessity, in a very much shorter form. Ours is the first book of its kind, one which discusses a specific aspect of all spiders' lives, and so increases our knowledge of this interesting group of animals.

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